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99E-102

4.5 PSP Cover Sheet (Attach to the front of each proposal)

Proposal Title: Determining substrate requirements for passive interdiction and population control of migrating Chinese mitten crabs

Applicant Name: Clifford A. Hui
Mailing Address: USGS/Davis Field Station, 1 Shields Ave, UC Davis, Kerr Hall, Room 278, Davis CA 95616
Telephone: (530) 752-6420
Fax: (530) 752-8561
Email: cliff_hui@usgs.gov

Amount of funding requested: $ 286,829 for 2 years

Indicate the Topic for which you are applying (check only one box).

- ☐ Fish Passage/Fish Screens
- ☐ Habitat Restoration
- ☐ Local Watershed Stewardship
- ☐ Water Quality
- ☒ Introduced Species
- ☐ Fish Management/Hatchery
- ☐ Environmental Education

Does the proposal address a specified Focused Action? _____ yes XXXXX no

What county or counties is the project located in? Yolo

Indicate the geographic area of your proposal (check only one box):

- ☐ Sacramento River Mainstem
- ☐ Sacramento Trib: ______
- ☐ San Joaquin River Mainstem
- ☐ San Joaquin Trib: ______
- ☐ Delta: ______
- ☐ East Side Trib: ______
- ☐ Suisun Marsh and Bay
- ☐ North Bay/South Bay: ______
- ☒X Landscape (entire Bay-Delta watershed)
- ☐ Other: ______

Indicate the primary species which the proposal addresses (check all that apply):

- ☐ San Joaquin and East-side Delta tributaries fall-run chinook salmon
- ☐ Winter-run chinook salmon
- ☐ Late-fall run chinook salmon
- XX Delta smelt
- XX Splittail
- ☐ Green sturgeon
- ☐ Migratory birds
- XX Other: Chinese mitten crab
- ☐ Spring-run chinook salmon
- ☐ Fall-run chinook salmon
- ☐ Longfin smelt
- ☐ Steelhead trout
- ☐ Striped bass
- ☐ All chinook species
- ☐ All anadromous salmonids

Specify the ERP strategic objective and target (s) that the project addresses. Include page numbers from January 1999 version of ERP Volume I and II:

Native species recovery and conservation. V.I, p497; V.II, p110
Rehabilitation of natural ecosystem processes and habitats. V.I, p.40, p.467; V.II, p.73

Indicate the type of applicant (check only one box):

- ☐ State agency
- ☐ Public/Non-profit joint venture
- ☐ Local government/district
- ☐ University
- XX Federal agency
- ☐ Non-profit
- ☐ Private party
- ☐ Other: ______________

Indicate the type of project (check only one box):

- ☐ Planning
- ☐ Monitoring
- XX Research
- ☐ Implementation
- ☐ Education

By signing below, the applicant declares the following:

1.) The truthfulness of all representations in their proposal;

2.) The individual signing the form is entitled to submit the application on behalf of the applicant (if the applicant is an entity or organization); and

3.) The person submitting the application has read and understood the conflict of interest and confidentiality discussion in the PSP (Section 2.4) and waives any and all rights to privacy and confidentiality of the proposal on behalf of the applicant, to the extent as provided in the Section.

CLIFFORD A. HUI

Printed name of applicant

Clifford A. Hui

Signature of applicant

I. TITLE PAGE

Title of Project: **DETERMINING SUBSTRATE REQUIREMENTS FOR PASSIVE INTERDICTION AND POPULATION CONTROL OF MIGRATING CHINESE MITTEN CRABS**

Principle Investigator: Clifford A. Hui, Ph.D.
USGS, 278 Kerr Hall, University of California, 1 Shields Ave.,
Davis, CA 95616-5224
FAX: (530)752-8561; e-mail: cliff_hui@usgs.gov; ph: (530)752-6420

Type of Organization and Tax Status: Federal government / tax-exempt

Tax Identification Number: 530196958

Technical and Financial Contact Persons:
Technical: Clifford A. Hui
USGS, 278 Kerr Hall
University of California
1 Shields Ave.
Davis, CA 95616-5224
FAX: (530)752-8561; e-mail: cliff_hui@usgs.gov; ph: (530)752-6420
Financial: Sherry DuFault
USGS Biological Resources Division, WERC
California State University, Sacramento
6000 J Street, Placer Hall
Sacramento, CA 95819-6129
FAX: (916)278-3101; e-mail: sherry_dufault@usgs.gov; ph: (916)278-3252

Participants and Collaborators in Implementation:
Christina Swanson, Ph.D.
Aquatic Fishery & Research Facility at the University of California, Davis

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II. EXECUTIVE SUMMARY

The Chinese mitten crab, *Eriocheir sinensis*, may be one of the most dangerous invaders of the Sacramento and San Joaquin drainages to date. This species, first reported in the South Bay in 1992, has exhibited exponential population growth and now occurs in massive numbers. At current and anticipated population levels, these animals can severely affect the ecological balances within the San Francisco Bay/Delta watershed, levee stability, water conveyance and diversion projects, commercial and sport fisheries, habitat restoration and management efforts, and human health.

The mitten crab is catadromous: juvenile crabs walk upstream where they grow for 1-3 years and mature crabs walk downstream to spawn in the brackish waters of the San Francisco Bay/Delta. This migration pattern means that an entire year class moves through known bottlenecks in the drainage system. These bottlenecks offer an opportunity to interdict the migration and dispose of the crabs. This research proposal will provide necessary background information to develop passive interdiction pathways that lead to disposal depots.

The primary ecological objectives are to determine the substrates preferred and rejected by the crabs for walking. Under controlled conditions in a laboratory, crabs will be videotaped while offered paired choices of three substrates (smooth, rocky, muddy). Preferences will be determined through statistical analysis. Also, crabs will be videotaped while walking over the same three substrates and various walking parameters (e.g., step length, stance width, etc.) will be measured and compared among substrates. From these data, hypotheses will be developed as to what physical aspects of the substrates (e.g., mud stickiness, rock size, etc.) contribute to the preferences. A third set of experiments will consist of offering the crabs more paired choices of substrate but the substrates will have their physical characteristics manipulated to test hypotheses regarding the physical aspects contributing to preference/rejection of substrate. These results will provide information necessary for the design of pathways of preferred substrate bordered by rejected substrate to interdict migrating crabs and guide them to disposal depots.

Adult crabs will be collected at state and/or federal fish salvage facilities and the laboratory work will be conducted on the campus of the University of California at Davis in Yolo County. Because there is no field work component to this project, no environmental impacts will occur and there are no local programs requiring coordination. The duration of this project is anticipated to be 1.5 years (Sep 99 - Feb 01) but may be longer if funding is delayed because crab collection and walking behavior is dependent on migration season. Delayed funding may require extension of work through another fall migration season. The USGS will share costs if funding is from the US Department of Interior (DOI). In that case, costs to CALFED will be $286,828. The proposed work is compatible with CALFED objectives of recovery of at-risk native species, rehabilitating natural processes in the Bay-Delta system, improving recreational fishing, improving reliability of levee system, and reducing negative biological and economic impacts of established non-native species.

The Co-principal Investigators are members of the Mitten Crab Project Work Team (Hui participates in the Ecology Subgroup; Swanson participates in the Levee Subgroup) and participated in the development of the National Mitten Crab Management Plan Program. They both have extensive experience with aquatic animal behavior and locomotion and have worked in recent years in the San Francisco Bay/Delta. Both have Doctoral degrees in biology.

III. PROJECT DESCRIPTION

A. Proposed Scope of Work

Introduction. Invasion of the San Francisco Bay/Delta and its watershed by non-native species is one of the greatest threats to the overall health of the system. Invasion is also a serious threat to the success of habitat restoration and to native species conservation and recovery efforts. The Chinese mitten crab, *Eriocheir sinensis*, is feared to be one of the most dangerous invaders to date. This species, first reported in the South Bay in 1992, has exhibited exponential population growth and penetrated many miles upstream in both the Sacramento and San Joaquin drainages. The catadromous life history of the mitten crab amplifies its potential to affect many geographic areas within the system. The juveniles walk upstream where they grow over a period of 1-3 years. The mature crabs walk downstream in the fall to spawn in the brackish waters of the San Francisco Bay/Delta. The San Francisco watershed is compatible with the mitten crabs' natural history because, as indicated by preliminary field surveys (CDFG) and reports from the state and federal fish salvage facilities, the species now occurs in massive numbers. At current and anticipated population levels, they have the capacity to severely affect the Bay/Delta system in several areas including:

- **ecology** (e.g., predation and competition impacts on food webs and benthic communities, biomagnification of contaminants);
- **levee stability** (e.g., burrowing may impair levee structural integrity);
- **water conveyance and diversion** (e.g., migrating crabs clog urban, industrial and agricultural water diversions, and paralyze fish salvage operations at state and federal pumping facilities);
- **commercial and sport fisheries** (e.g., direct impacts on crayfish and shrimp fisheries, indirect effects on commercial and sport fisheries for chinook salmon, striped bass and American shad by reducing salvage of young fishes, and bait stealing for hook and line fisheries);
- **human health** (e.g., mitten crab may be a host for the Oriental lung fluke and may accumulate contaminants);
- **habitat restoration and management** (e.g., hamper native species recovery and conservation, reduce effectiveness of new fish screens).

Total eradication of the mitten crab may be impossible. Therefore, research and management efforts must be directed at developing effective, continuous, population reduction and control operations that do not negatively impact native species. Effective population control operations will require detailed understanding of the species' ecology and behavior (e.g., National Mitten Crab Management Plan, USFWS) but, to date, very little is known about this highly mobile invader. To begin filling this information gap, we propose a focused, applied research project to determine mitten crab substrate preferences by examining their locomotion and behavior. The results may be applied to devise guidance pathways (e.g., of a preferred substrate) to intercept and attract migrating crabs to collection depots.

Objectives and Approaches.

Objective 1: Determine substrate (mud, rocks, smooth) preferences of migrating mitten crabs.
Approach: Offer choices of substrates to crabs and determine selection pattern.

Objective 2: Determine characteristics of substrates that influence selection by the crabs.
Approach: Measure locomotion parameters (e.g., walking speed, step length) of walking crabs over different substrates and determine how those parameters change with different substrate

qualities (e.g., mud stickiness, rock size).
Objective 3: Apply results to help design minimally intrusive migration pathways to intercept, attract and guide mitten crabs to collection depots.
Approach: Use results of Objectives 1 & 2 to select optimum substrates for path (preferred) and boundaries (rejected) for an interdiction pathway.

Methods. Adult Chinese mitten crabs will be collected from the state and/or federal fish salvage facilities in the south Delta. Experiments on substrate preference and locomotion will be conducted at the Aquaculture and Fisheries Program Aquatic Research Center, University of California, Davis. This three-phase project will extend over two winter migrations of the mitten crab. These phases are interdependent, providing components necessary for the design of minimally intrusive migration pathways to intercept, attract and guide mitten crabs to collection depots. Project management will be conducted by the Principal Investigator.

Phase I, Sep 99-Feb 00: Construct test apparatus; collect mitten crabs; collect data on substrate preference, locomotion, and tested substrate qualities.

Phase II, Mar 00-Jul 00: Analyze data from preference, locomotion and substrate quality studies; conduct substrate quality manipulation studies; develop substrates with qualities designed to enhance selection.

Phase III, Aug 00-Feb 01: Collect mitten crabs; collect data on substrate preference and locomotion on altered substrates; analyze data; prepare written and videotape reports.

B. Location and geographic boundaries

The stressors, habitats, and species addressed by this project are located in all areas within the Sacramento-San Joaquin watershed, estuary, and San Francisco Bay where mitten crabs have been reported. Application of the results of this project, development of guidance pathways for mitten crab collection and disposal, will have greatest benefit along known mitten crab migration corridors, e.g., lower Sacramento and San Joaquin rivers, and/or upstream of federal and state fish salvage facilities.

IV. ECOLOGICAL/BIOLOGICAL BENEFITS AND TECHNICAL JUSTIFICATION

A. Ecological/Biological Objectives

Population control of established invasive species has been identified by CALFED as a major strategic plan goal. This goal is essential to safeguard planned and ongoing habitat restoration efforts, to protect of native species and, in the case of Chinese mitten crabs, to protect levee integrity for water conveyance, water quality, and flood control. Mitten crabs, because of their rapid population growth and potential impacts on multiple aspects of the Bay/Delta system and watershed, pose an extremely serious threat to the ecological and functional integrity of the system. Development of effective population control strategies and methods requires detailed understanding of the target organism's biology, ecology, physiology, and behavior (National Mitten Crab Management Plan, USFWS). However, despite previous mitten crab invasions in other aquatic systems (e.g., Europe), very little other than a basic understanding of the species' natural history is known about the species in general, and even less about its biology within the Bay/Delta system. The objective of the proposed project is to investigate a critical aspect of mitten crab natural history and behavior, locomotion and substrate preference, and to use the results to develop an efficient, effective population control strategy that has minimal adverse impacts on native species and their habitats. Listed below are the technical justifications for the project approach and proposed population control strategy.

1. Mitten crabs are highly mobile and undertake age-determined migrations; juvenile crabs migrate upstream (spring-summer) and maturing adults migrate downstream during a relatively narrow temporal window (fall-winter) to brackish water for spawning. These directed migrations, in which the entire population of a particular year-class must transit a limited number of routes, present the most practical time for concerted population control efforts.

2. Comprehensive and quantitative understanding of mitten crab locomotion, the effects of substrate type on locomotion, and their substrate preferences for locomotion will contribute to our understanding of migration routes, maximum migration distances, and will suggest ways to intercept and guide migrating crabs to collection sites for removal (e.g., using a traveling screen similar to that undergoing tests at the Tracy Fish Facility, USBR) and disposal.

3. Outmigrating adult crabs, which are moving from an extremely large geographic distribution in the Delta and tributary rivers downstream to the more constricted confluence, would probably be the best target for population control efforts for several reasons:

a. increased probability of intercepting, diverting, collecting, and disposing of a large portion of the population as the crabs pass through migration bottlenecks;

b. adult crabs are the most serious threat to fish salvage at the state and federal facilities; and

c. reduction in numbers of adult crabs reduces spawning population size and thus reduces population sizes of succeeding generations.

4. Effective population control of the mitten crab will probably be a continuous program, thus development of a method that has minimal impacts on habitats and native species is crucial.

5. Collection and removal of crabs focused at the state and federal fish salvage facilities, while necessary to protect salvaged fishes, will not significantly affect mitten crab population levels because migrating crabs collected at the facilities represent only a small fraction of the adult population.

B. Linkages

Chinese mitten crabs were only recently determined to present a serious threat to the Bay/Delta system, thus there are no past or ongoing CALFED programs directed at the species. The proposed project is new and complements several ongoing and proposed research efforts, including studies of distribution, habitat utilization, and burrowing. In particular, this project, with its emphasis on substrate preference and locomotion, directly complements ongoing research on collection and diversion methods of migrating crabs at the federal fish facilities (USBR).

In addition to development of population control measures for established **invasive species** (CALFED Goal 5; ERPP, Volume 1, p. 40, 467; Vol. 2, p. 73), the proposed project addresses other CALFED and ERPP goals including:

- **native species recovery and conservation** - mitten crabs have disastrous effects on fish salvage operations at state and federal facilities (CALFED Goal 1; ERPP Vol 2, p. 110; Vol 1, p. 497)
- **rehabilitation of natural ecosystem processes and habitats -** 1) mitten crabs compete with native species for habitat and food, prey upon native species, and alter natural habitats by burrowing; and 2) adverse effects of invasive species like the mitten crab can negate the positive effects of habitat and ecosystem restoration and operational improvement (e.g., fish screens and fish salvage) programs (CALFED Goals 2 and 4; ERPP Vol. 1, p. 40, 467; Vol. 2, p. 73)
- **recreational and commercial species** - mitten crabs disrupt shrimp and crayfish

fisheries, threaten the dungeness crab fishery, kill salvaged commercial and sport fishes (e.g., chinook salmon, striped bass, American shad), and steal bait (CALFED Goal 3).

- **levee system integrity** - burrowing behavior of mitten crabs may impair levee structural integrity, threatening water supply, water quality, flood control, Delta and upstream land use and associated economic activities, and the ecosystem from catastrophic failure (CALFED Bay/Delta Program Objective).

C. System-wide Ecosystem Benefits

By its sheer numbers the Chinese mitten crab is having a serious impact in the San Francisco Bay/Delta ecosystem. It is impairing fish salvage operations at state and federal facilities and thus on recovery and conservation of priority species (e.g., delta smelt, splittail, chinook salmon) and threatens to disrupt benthic communities, to alter food webs, and to reduce effectiveness of new fish screens (e.g., impairing flows through screens, clogging bypasses). As a potential host and vector of the Oriental lung fluke and as a possible bioaccumulator of toxic compounds and metals, it may be a serious hazard for human (and animal) consumption. Other negative effects may yet be reported as more information becomes available about mitten crabs within the Bay/Delta system and Sacramento-San Joaquin watershed. Improved understanding of mitten crab natural history and the results of this proposed focused applied investigation of their movement will provide integral components for development of effective population control strategies that do not jeopardize other ecosystem restoration programs and have minimal impacts on native species.

D. Compatibility with Non-Ecosystem Objectives

Unlike many other established invaders that largely affect the Bay/Delta and watershed ecology and food webs, the mitten crab also poses a credible threat to a number of non-ecosystem related issues. Results and applications of this project to control mitten crab populations will provide benefit for several CALFED non-ecosystem objectives including: levee system integrity (burrowing behavior may weaken levees); water quality (levee failures could result in increased salt water intrusion into the Delta and reduced quality of diverted water); water supply (problems with fish salvage may force reductions in pumping rates; mitten crabs may also affect screened and unscreened industrial, urban, and agricultural diversions); and commercial and sport fisheries (e.g., shrimp, crayfish, dungeness crab, chinook salmon, striped bass, American shad).

V. TECHNICAL FEASIBILITY AND TIMING

The methodology described in this proposal will provide the information necessary to meet the stated objectives. Not only will substrate preferences be determined but the substrate characteristics that induce those preferences will be identified. Such information may be critical when construction of interdiction pathways is initiated. No other alternatives are known that will meet the same objectives.

The ultimate objective (to be pursued under a subsequent effort) is to construct effective interdiction pathways. Currently, these pathways are envisioned to consist of the most-preferred substrate bordered by the least-preferred, or rejected, substrate. Because the walking behavior of the crabs is predictable only during migration (downstream), these pathways will be functional only during the migration period in the fall (August - November). Effects of siltation during these few months will be much less than if the effort were required to be functional all year.

However, stream flow and stream bottom vary considerably throughout the San Francisco Bay/Delta system so some locations are better suited for interdiction pathways than others. Also, the optimum pair of substrates (path and border) may not work at a given location for any number of reasons. In such cases, interdiction effectiveness with other substrates can be estimated (and determined to be worthy of effort or not) based on the results of Phase III of the proposed project. Details on how and where such an interdiction system will function is dependent on the physical characteristics of candidate sites and on the results of this project.

This project will occur in a laboratory setting and requires no CEQA, NEPA, or other environmental compliance documents. Permits required to be in place to proceed with this project are CDFG Scientific Collecting Permit (FG 1379) and CDFG Restricted Species Permit (FG 1312). Applications for both permits have been submitted. No zoning regulations, planning ordinances or other constraints that could impact the schedule and implementability of the project are known.

VI. MONITORING AND DATA COLLECTION

A. Biological/Ecological Objectives

The objective is to determine the type of substrate on which mitten crabs prefer to walk. Previous work (reprint enclosed) showed that the lined shore crab *Pachygrapsus crassipes*, closely related to the mitten crab (same family), changed locomotory parameters (e.g., mean walking speed, duty factor, stance width) when walking on different substrates. That work will serve as a model for the proposed project. We hypothesize that the mitten crab will demonstrate similar changes and these changes will be indicative of preference for types of substrate. We will then determine the preferences, modify the substrate to enhance/reduce key characteristics, and measure changes in strength of preferences. Data on preferred and rejected substrates can then be used to design paths for interdiction of migrating mitten crabs. The major limitation of this study is the narrow time window in which crabs will be available. If funding is delayed, testing may need to be extended to another year to include another migration.

B. Monitoring Parameters and Data Collection Approach

This study will be executed in a laboratory so no habitat monitoring is needed. Test animals will be collected at fish salvage facilities in the south Delta during the fall downstream migration and relocated to the University of California, Davis, for the experiments. Experiments will be conducted in a test flume constructed for this project. In the flume, flowing water will induce directed walking behavior. After the tests, the crabs will be disposed of as required by the CDFG Restricted Species Permit.

Parameters/measurements: substrate type (smooth, rocky, mud); substrate quality (stickiness, roughness); locomotion (walking speed, time dactylus moves on and off the substratum, length of each step, stance); substrate preference (proportion of time on each substrate, distance and proportion of total distance traveled on each substrate).

Data Collection: All locomotion and substrate preference experiments will be videotaped to produce a permanent record. In preference experiments, each crab will be presented paired choices of substrate. Substrate quality data will be measured using appropriate instruments.

C. Data evaluation approach

Sample size: Locomotion and substrate preference data will be collected on a minimum of 10 adult crabs. In locomotion experiments, each crab will walk on each of three substrates (flat, rocky, muddy) enough times to provide five analyzable sequences. In substrate preference experiments, each crab will be tested a minimum of 10 times on each paired substrate choice.

Locomotion: Walking parameters will be measured from videotape records using a computer-assisted, video-capture, motion analysis system (Peak Performance Technologies, Inc.). Results will be analyzed using comparative statistics (e.g., ANOVA, regression analysis).

Substrate preference: Proportion of time on each substrate, distance and proportion of total distance traveled on each substrate will be measured manually from videotape records. Results will be analyzed using appropriate statistics (e.g., ANOVA, binomial, Chi square).

D. Reports

Quarterly reports will include financial status, activities during the quarter, tasks completed, deliverables produced, problems encountered, and a description of modifications to the contract. The final technical written report also will be published in scientific journals where peer review assures adherence to current scientific standards. Videotape records will also be provided to CALFED and made available to interested agencies. All data will be stored by the Principal Investigator for five years after project completion. These data may have only limited use for metadata. There are no existing data sources to support this project.

Table 1. Monitoring and Data Collection Information

Biological/Ecological Objectives			
Hypothesis/Question to be Evaluated	Monitoring Parameter(s) and Data Collection Approach	Data Evaluation Approach	Comments Data Priority
(1) How do walking parameters change on each of several different substrates?	Videotape crabs walking on mud, flat, and rocky substrates and measure walking speed, time each dactylus moves on and off the substratum, length of each step, and stance width.	Compare duty factor, stance width, phase difference between leading and trailing rows, and walking speed among substrates.	Essential data to address Question (3).
(2) What is the relative degree of preference for each of the tested substrates?	Videotape crabs when presented with paired choices of substrates to walk on. Each crab to make clear selections in at least 10 trials.	Use appropriate statistics to determine preferences.	Essential data to address Question (3).
(3) What are the mechanical parameters of each substrate type which make it more/less preferred?	Videotape crabs when presented with paired choices of modified substrates to walk on. Each crab to make clear selections in at least 10 trials.	Use appropriate statistics to determine preferences and compare with results of Question (2).	Will be basis to design pathways for interdiction of migrating mitten crabs.

VII. LOCAL INVOLVEMENT

This project will perform measurements on walking of mitten crabs while in a controlled environment. When it is evident that execution of field tests will be fruitful, they will be conducted under the umbrella of a separate funding effort. To conduct the proposed measurements, it is not necessary for the participation, consent, or endorsement of local agencies, environmental groups, property owners, or facility owners, or to perform public outreach. However, we have notified the Yolo Country Board of Supervisors and the Yolo County Planning Department about our proposal submission (copies of letters are attached).

VIII. COST

A. Budget

The budget in Tables 2 and 3 reflects costs and USGS cost sharing, assuming that CALFED funds are from sources within the US Department of Interior (DOI). The Project Management Task consists primarily of validation of costs, preparation of periodic reporting requirements, response to project-specfic questions, and necessary costs directly associated with project oversight. Costs for this task are labor and report preparation.

Table 2. Total Budget (CALFED funds only) assumes funding is from *US Department of Interior*.

Task	Direct Labor Hours	Direct Salary and Benefits	Service Contracts	Material and Acquisition Costs	Misc. and other Direct Costs	Overhead and Indirect Costs	Total Cost
Phase I	1,186	50,974	300	45,000	11,552	0	107,827
Phase II	2,343	104,131	400	1000	14,403	0	119,934
Phase III	*888*	*39,107*	*900*	*1200*	*5,771*	0	*46,978*
Project Management Task	263	10,241	0	0	1,849	0	12,090

Table 3. Quarterly Budget assumes CALFED funding is from US Department of Interior.

Task	Quarter Budget Jul - Sep 99	Quarter Budget Oct - Dec 99	Quarter Budget Jan - Mar 00	Quarter Budget Apr - Jun 00	Quarter Budget Jul - Sep 00	Quarter Budget Oct - Dec 00	Quarter Budget Jan-Mar 01	Total Budget
Phase I	77,421	32,658	0	0	0	0	0	110,079
Phase II	0	36,569	28,456	28,456	28,456	0	0	121,937
Phase III	0	0	0	0	0	*27,278*	*27,535*	*54,813*
Total	77,421	69,227	28,456	28,456	28,456	27,278	27,535	286,829

I-019651

B. Schedule
Specific tasks will have the start/completion dates noted below:

Table 4. Proposed work schedule.

Phase	Start Date	Completion Date
Phase I: Construct test apparatus; collect mitten crabs; collect data on substrate preference, locomotion, and tested substrate qualities.	01 Aug 99	29 Feb 00
Phase II: Analyze data from preference, locomotion and substrate quality studies; conduct substrate quality manipulation studies; develop substrates with qualities designed to enhance selection.	01 Mar 00	31 Jul 00
Phase III: Collect mitten crabs; collect data on substrate preference and locomotion on altered substrates; analyze data; prepare written and videotape reports.	01 Aug 00	28 Feb 01

IX. COST SHARING

With project funding assumed to originate from within the US Department of Interior (DOI), the USGS will contribute overhead charges (16%). A cost savings of over $45,000 will be realized compared to funding from a non-DOI source.

X. APPLICANT QUALIFICATIONS

This project will have a small staff, consisting of the Principal Investigator and Co-Principal Investigator. The Principal Investigator will be responsible for administration and management of the project. Both investigators will share technical and execution responsibilities.

Both investigators are members of the Mitten Crab Project Work Team (Hui participates in the Ecology Subgroup; Swanson participates in the Levee Subgroup) and participated in the National Mitten Crab Management Plan Program. Both investigators have extensive experience with aquatic animal behavior and locomotion and have worked in recent years in the San Francisco Bay/Delta.

Biosketches:

Clifford A. Hui

BA (zoology) Pomona College 1967
MA (biology) San Diego State University 1973
Ph.D. (environmental physiology) UCLA 1983
Current position: Research Biologist (GS-13), USGS, Davis, California.

Relevant publications:

Maneuverability of the Humboldt penguin (*Spheniscus humboldti*) during swimming. Canadian Journal of Zoology 63:2165-2167 (1985).

Porpoising behavior of penguins: energy conservation or respiratory necessity? Canadian Journal of Zoology 65:209-211 (1987).

Penguin Swimming I. Hydrodynamics. Physiological Zoology 61:333-343 (1988).

Surfacing behavior and ventilation in free-ranging dolphins. Journal of Mammalogy 70:833-835 (1989).

Walking of the shore crab *Pachygrapsis crassipes* in its two natural environments. Journal of Experimental Biology 165:213-227 (1992).

Elemental contaminants in the livers and ingesta of four subpopulations of the American coot (*Fulica americana*): an herbivorous winter migrant in San Francisco Bay. Environmental Pollution 101:321-329 (1998).

Christina Swanson

BA (biology) Cornell University 1980
Ph.D. (biology) UCLA 1991
Current position: visiting post-doctoral researcher, Department of Wildlife, Fish, and Conservation Biology, University of California, Davis.

Recent publications:

Swimming performance of delta smelt: maximum performance, and behavioral and kinematic limitations on swimming at submaximal velocities. Journal of Experimental Biology. 201:333-345 (1998); with P. S. Young and J. J. Cech, Jr.

Performance, behavior, and physiological responses of Delta fishes in two-vector flows in a fish treadmill. Part 3. Biological studies using the fish treadmill. Final Report, California Department of Water Resources. 59 pp. (1998); with P. S. Young and J. J. Cech, Jr.

Interactive effects of salinity on metabolic rate, activity, growth and osmoregulation in the euryhaline milkfish (*Chanos chanos*). Journal of Experimental Biology 201:3355-3366 (1998).

Comparative environmental tolerances of threatened delta smelt (*Hypomesus transpacificus*) and introduced wakasagi (*H. nipponensis*) in an altered California estuary (1999); with T. Reid, P. S. Young, and J. J. Cech, Jr. (submitted, manuscript available on request)

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WALKING OF THE SHORE CRAB *PACHYGRAPSUS CRASSIPES* IN ITS TWO NATURAL ENVIRONMENTS

By CLIFFORD A. HUI*

Chemistry and Biochemistry Branch, Code 521, Naval Ocean Systems Center, San Diego, CA 92152-5000, USA

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Summary

Video analyses of crabs walking on smooth and rocky terrains when in air and when submerged in water were conducted. Modifications of walking in the two environments, between which the animal's weight changes sixfold, are consistent with the goals of maximizing ease of walking and minimizing risk of injury. The duty factor (fraction of step cycle in which the dactylus is in contact with the substratum) was greater than 50 % when in air compared to less than 46 % when submerged, indicating a need for greater stability against the destabilizing vertical force of gravity when in air. The duty factors of the trailing and leading leg rows were the same for the two terrains in air but the trailing leg row had a larger duty factor when submerged, indicating a greater pushing effort to overcome drag forces. Width of stance differed among the four conditions and was narrowest in animals walking over rocky terrain in air, the condition which has the greatest potential for injury. The mean phase difference (percentage of a step cycle by which ipsilateral legs differ) between leading and trailing rows did not differ under any condition except for submerged smooth terrain, meeting the unique requirements of that condition. The observed walking speed range had no effect on stance, duty factor or phase difference.

Introduction

Shore crabs inhabit two environmental regimes while their brachyuran relatives inhabit only one. There is no shore crab more successful than the lined shore crab *Pachygrapsus crassipes* Randall. This crab is found along rocky shores on the west coast of North America from 24°20′ to 45° latitude and in Japan and Korea between 34° and 37° (Hiatt, 1948). Its habitat extends from the upper low intertidal zone to the highest high intertidal zone (Hiatt, 1948), and the crab has been maintained out of water for up to 4 days (Gross, 1957).

An important element in the successful competition of *P. crassipes* is locomotion. Locomotion enables migration (Bovbjerg, 1960*a*; Gross, 1961), foraging

*Present address: U.S. Fish & Wildlife Service, c/o Wildlife & Fisheries Biology Department, University of California, Davis, CA 95616, USA.

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(Hiatt, 1948), courtship (Bovbjerg, 1960*b*) and predator escape (Hiatt, 1948). All these activities, except courtship, occur in both air and water. However, the physical requirements for locomotion differ between the two regimes. In air, it is the vertical force of gravity that may destabilize (cause loss of control) a walking crab, but in water, buoyancy neutralizes the effects of gravity and it is the horizontal forces of currents or drag resistance that are destabilizing.

These crabs may change locomotion variables to accommodate the different physical constraints of each regime. Other animals change locomotion patterns to minimize energy expenditure (Hoyt and Taylor, 1981; Dawson and Taylor, 1973), maximize ventilation (Jackson and Prange, 1979; Carrier, 1987; Hui, 1987, 1989) or reduce mechanical stresses (Farley and Taylor, 1991). Some spiders have different walking patterns when walking on land to those when walking on water (Schultz, 1987). In the light of these observations and because a change in environmental regime triggers a change in social behaviour of *P. crassipes* (Bovbjerg, 1960*a*), it seems reasonable to expect that a change in environmental regime, with its concomitant change in physical forces, would also trigger a change in locomotory patterns.

There are many studies of walking crustaceans (e.g. Pond, 1975; Barnes, 1975; Chasserat and Clarac, 1980; Grote, 1981; Hessler, 1982; Clarac *et al.* 1987; Blickhan and Full, 1987; Muller and Clarac, 1990*a*,*b*), but the nature of modifications in locomotion effected in compensation for changes in normal environmental conditions has not been thoroughly explored. I report here on the differences in locomotion patterns of *Pachygrapsus crassipes* walking in the two environmental regimes and two terrains of its normal habitat.

Materials and methods

Animals

Male *Pachygrapsus crassipes* were collected at Hospitality Point on Mission Bay in San Diego, California, using bait on a line during the month of August. Only the largest individuals with all appendages intact were retained for recording. The range for the maximum widths of the carapaces was 33.6–38.8 mm, well above the 14.0 mm width of minimum size for sexual maturity (Hiatt, 1948). The animals were maintained in aerated sea water at collection site temperature but not fed. All recordings were completed and the crabs released within 26 h of capture. Eight crabs were used for recording.

Recording

Video recordings (Panasonic WV–F2 camera, Panasonic AG2400 recorder, at 30 frames s^{-1}) of the crabs were made using a mirror arrangement enabling a vertical view (Fig. 1). Each crab was placed in a plastic pan (47 cm×35 cm×12 cm deep) under one of two regimes: in air or submerged in sea water. In each submerged case the water was of a depth (approximately 9 cm) adequate not only to cover the crab but also to preclude the formation of surface ripples (energy

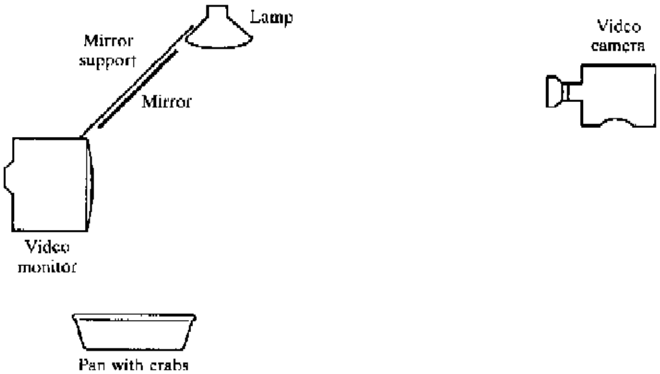

Fig. 1. Schematic drawing (not to scale) showing the general configuration of the observation set-up.

consuming) when the crab was walking. Each regime had two terrains: smooth (a large paper towel was fastened to the bottom for traction) and rocky. The rocky substratum consisted of several layers of randomly placed broken quartz-like material. The thickness of the layers was adequate to ensure that, if a space between rocks opened directly to the floor of the plastic pan, the distance was greater than the reach of the crab's leg. The broken nature of the rocks and their random placement ensured an irregular walking surface. The rocks had a mean maximum length (±S.D.) of 42.8±9.9 mm and mean maximum width of 30.5 ±7.8 mm (N=20). The third dimension was the smallest but was not measured because the first two dimensions will impart the nature of the rocky terrain. Although not the dark type of the crabs' natural habitat, this rock contrasted with the dark body colour of the crabs and facilitated video analysis.

Each crab was individually recorded walking over both terrains (one at a time) of only one of the regimes. A minimum of five walking sequences for each terrain for each crab was selected for analysis. Criteria for selection were a straight path, an even sideways gait and clarity of the images. Ground contact by the dactylus is evident because (1) horizontal displacement ceases and (2) the dactylus changes orientation from vertical to horizontal. A mark of known length was placed in the camera's view for each walking session and used for scaling adjustments. Measurements were taken directly from a 48-cm (diagonal) video screen. The stop-action capability of the player (Panasonic AG500) and the on-screen time record allowed reacquisition of the same images for re-examination when necessary.

The data collected were the mean walking speed, the time that each dactylus moved onto and off the substratum, the length of each step (distance between the substratum contact points for a dactylus) and stance (maximum distance between the dactyli of a contralateral leg pair within one step sequence). The stance measurement did not require that both dactyli of the pair be on the substratum simultaneously. The number of steps measured for each dactylus for each walking sequence varied from 0 to 7.

Buoyancy

The weights of this species of crab in water and in air were determined using 13 individuals not used in the locomotion recordings. The range of the maximum carapace widths was 26.9–35.3 mm. The crabs were divided into two groups (mean carapace widths: 32.00±2.38 mm, 34.05±1.23 mm) and the individuals in each group were weighed together as a single group in both air and water. Weighing them as groups increased the total weight, thereby reducing relative error.

Results

Eighty-two walking sequences were examined: 32 in air (3 crabs, 17 sequences on smooth terrain, 15 sequences on rocky) and 50 submerged (5 crabs, 25 sequences each on smooth and rocky terrain). Occasionally a crab walked forwards, backwards or obliquely or turned, but these sequences were not considered. Sample size was inadequate for paired comparisons. On careful observation, the fourth (last) leg on each side appeared to be used as a tactile sensor too frequently to be considered a participant in the general walking pattern displayed by the other legs (Fig. 2). Statistical results were more random when data from the fourth legs were included. Therefore, the results presented here exclude data from the fourth legs unless otherwise noted. The crabs displayed the various gaits expected by Wilson (1966) at the higher walking speeds for insects although the crabs were walking slowly. The alternating tripod gait Wilson described for the highest speeds occurred in crabs as the alternating tetrapod gait but appeared at the slowest speeds. The crabs never appeared to stumble. When a dactylus mis-stepped into a hole on rocky terrain, the leg continued through the stepping motion cycle until it made contact with the substratum.

At a constant framing rate of 30 frames s^{-1}, the relative precision of the timing measurements decreases as the walking speed increases. Using the relationships among stepping frequency, framing rate and maximum error described in error analysis for stepping locomotion (Ward and Humphreys, 1981), the maximum error at the fastest walking speed I measured (41.2 cm s^{-1}) is 9.3 % of the step duration. The maximum error of the 85 % of the total walking speeds that were below 12 cm s^{-1} (Fig. 3) is well within the 4 % error considered acceptable. The mean errors are half of the maximum error values (Ward and Humphreys, 1981). The variability in precision does not bias the measurement estimate systematically in any direction but increases the variance about the mean or presumed true value. Accordingly, none of my analyses regarding the time measurement is dependent on the precision of a given set of measurements. The analyses consist of

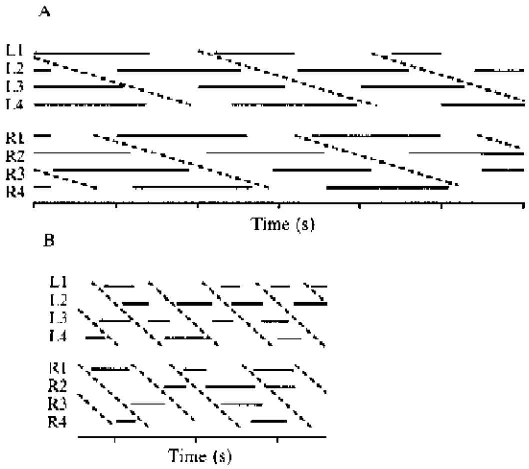

Fig. 2. Examples of stepping patterns. Solid lines indicate that the dactylus is in contact with the substratum. Dotted lines separate metachronal sequences. Metachronal sequences can be depicted as starting with the last leg, as described by Wilson (1966) for insects, instead of the first leg, but the slow walking speed data for crabs do not support the walking sequence paradigm presented by Wilson based on slow speeds. Marks on the time axis denote 1-s intervals. Individual legs are denoted on the left margin (L1 and R1 are the most anterior legs on the left and right sides, respectively). (A) Classic metachronal pattern; air regime, smooth terrain; speed=2.1 cm s^{-1}. (B) Metachronal pattern with inconsistent participation of various legs; submerged regime, rocky terrain; speed=6.1 cm s^{-1}. The duty factor is essentially the same for the two leg rows (39.4 % and 39.5 %) when all eight legs are considered, but when the fourth legs of each row are eliminated the leading row has a duty factor of 39.8 % while the trailing row has a factor of 44.0 %. The change may reflect the time for tactile exploration by the legs of the leading row. Note the 'missing' steps as dactyli are held off the substratum.

comparisons of means using non-parametric tests so that equality of variances of the tested groups is not required.

Owing to distortion near the edge of the screen, no measurements were taken within 8 % of the distance to the margin. No other measures were taken to compensate for possible distortion due to screen curvature. Repeated examination of several sequences resulted in duplication of length measurements to within 1 mm. Therefore, length measurement errors are considered to be negligible. Length data analyses also used non-parametric tests.

Speeds of the four conditions differed among each other (two-sided Mann–Whitney test, $P<0.02$) except that the speeds on the two terrains of the submerged regime were the same (two-sided Mann–Whitney test, $P>0.38$; Fig. 3). The range of speeds was greatest in air on smooth terrain but smallest in air on rocky terrain (Fig. 3).

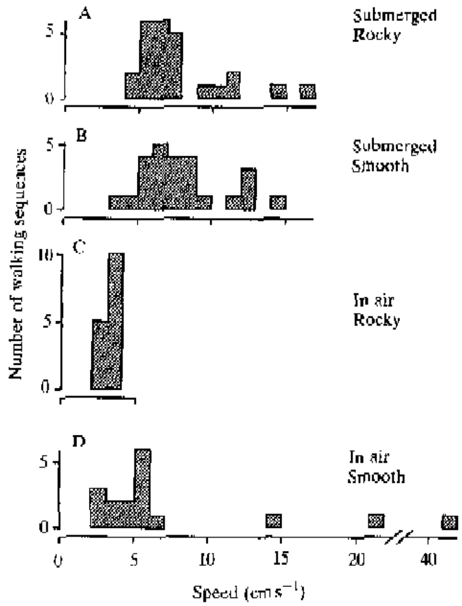

Fig. 3. Distribution of observed walking speeds among the various test conditions: (A) submerged regime, rocky terrain (mean=7.6 cm s^{-1}, S.D.=3.0 cm s^{-1}; (B) submerged regime, smooth terrain (mean=8.0 cm s^{-1}, S.D.=2.8 cm s^{-1}); (C) air regime, rocky terrain (mean=3.0 cm s^{-1}, S.D.=0.5 cm s^{-1}); (D) air regime, smooth terrain (mean=8.3 cm s^{-1}, S.D.=9.8 cm s^{-1}). Caution must be used against over-interpretation of speed frequency distribution data because data collection was optimized for stepping data, not speed distribution.

Stepping frequency is more closely correlated with walking speeds than is step length for every condition except the case of the leading leg row in air over rocky terrain (Table 1). The relative importance of frequency and length between the leading row and trailing row of legs differs between terrains of each regime (Table 1). The relationships of walking speed to stepping frequency are fitted to power functions (Table 2; Figs 4, 5, 6, 7); at the higher speeds the relationships approach a straight line and at walking speeds of 0 cm s^{-1} the stepping frequencies are zero. In the one condition for which speed is better correlated to step length, that relationship is also a power function (Table 1).

The ratios of the step lengths between the leading and trailing leg rows are the same for all the conditions except for walking in air on rocky terrain (Table 3). These ratios do not change with walking speed under any of the four conditions (r^2 range 0.06–0.46). A summary of the step length data is presented in Table 4.

The metachronal pattern (Fig. 2) was quantified by measuring the mean phase difference of the step cycle among adjacent ipsilateral legs (Table 1). The pattern

Table 1. *Some walking variables of* Pachygrapsus crassipes *leg rows in different walking conditions*

Condition (regime, terrain, leg row, N)	Phase differences* (% ±S.D.)	Frequency† (r)	Length‡ (r)	Duty factor§ (% ±S.D.)
Air, smooth, leading, 17	50.1±18.1	0.98	0.17	50.7±7.2
Air, smooth, trailing, 17	45.6±12.2	0.98	−0.20	54.8±5.8
Air, rocky, leading, 15	47.3±13.3	0.67	0.70¶	55.6±4.4
Air, rocky, trailing, 15	41.5±7.2	0.78	0.17	53.1±6.1
Submerged, smooth, leading, 25	43.8±8.3	0.92	0.10	40.7±4.5
Submerged, smooth, trailing, 25	49.8±7.6	0.90	0.47	45.9±5.8
Submerged, rocky, leading, 25	47.0±13.2	0.79	0.61	39.7±4.9
Submerged, rocky, trailing, 25	46.7±10.1	0.94	−0.06	42.3±5.0

Only the anterior six walking legs are considered.
N, number of sequences.
*Mean phase differences.
†Correlation of walking speed with stepping frequency.
‡Correlation of walking speed with step length.
§Mean duty factor.
¶Regression data: step length (mm) = $22.49 \times \text{speed}^{0.55}$ (cm s^{-1}).

Table 2. *Regression coefficients for stepping frequency (steps s^{-1}) as a function of walking speed (cm s^{-1})*

Condition (regime, terrain, leg row)	a	b	R	N
Air, smooth, leading	0.22	0.91	2.6–41	17
Air, smooth, trailing	0.27	0.76	2.6–41	17
Air, rocky, leading	0.43	0.48	2.1–3.8	15
Air, rocky, trailing	0.26	0.84	2.1–3.8	15
Submerged, smooth, leading	0.18	0.98	3.7–14.7	25
Submerged, smooth, trailing	0.26	0.82	3.7–14.7	25
Submerged, rocky, leading	0.38	0.64	4.1–16.8	25
Submerged, rocky, trailing	0.25	0.91	4.1–16.8	25

Regression coefficients are for the relationship $y = ax^b$.
Only the anterior six walking legs are considered.
R, speed range.
N, number of sequences.
Degrees of freedom = $N-2$ in each case.

did not differ between leading and trailing leg rows for three of the conditions (two-sided Mann–Whitney test, P>0.42), but the trailing leg row had a significantly greater phase shift than the leading row on the smooth terrain of the submerged regime (two-sided Mann–Whitney test, P<0.008). The phase difference did not change with the walking speeds I measured under any condition for either the leading or trailing leg rows (r^2 range 0.00–0.24).

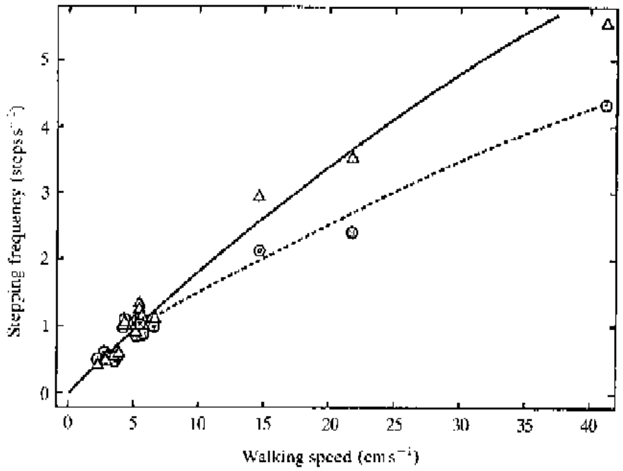

Fig. 4. The relationship of stepping frequency to walking speed for shore crabs travelling over smooth terrain in air. Triangles and solid line are for the leading leg row; circles and dashed line are for the trailing leg row; equations describing lines are given in Table 2; sample size is 17; each point represents an average value computed from 7–15 steps (mean=10.1 steps; S.D.=1.86 steps).

Table 3. *Step-length ratios of leading:trailing leg rows and the stance width*

Condition (regime, terrain, N)	Step-length ratios	Stance width (mm)
Air, smooth, 17	1.05±0.12	130.2±16.2
Air, rocky, 15	0.90±0.11	79.6±8.5
Submerged, smooth, 25	1.15±0.19	111.7±9.1
Submerged, rocky, 25	1.07±0.19	103.9±8.9

Values are mean±S.D.
Only the anterior six walking legs are considered.
N, number of sequences.

The duty factor (fraction of the step cycle in which the dactylus is in contact with the substratum) of the leading row was less than that of the trailing row in the submerged regime (two-sided Mann–Whitney test, $P<0.01$ over smooth terrain and $P<0.04$ over rocky terrain). In the air regime the duty factors between leg rows were the same (two-sided Mann–Whitney test, $P>0.07$ over smooth terrain and $P>0.26$ over rocky terrain). In air, the duty factor of the trailing leg rows over the two terrains is the same (two-sided Mann–Whitney test, $P>0.57$), but it is greater in the leading row over rocky than over smooth terrain (two-sided

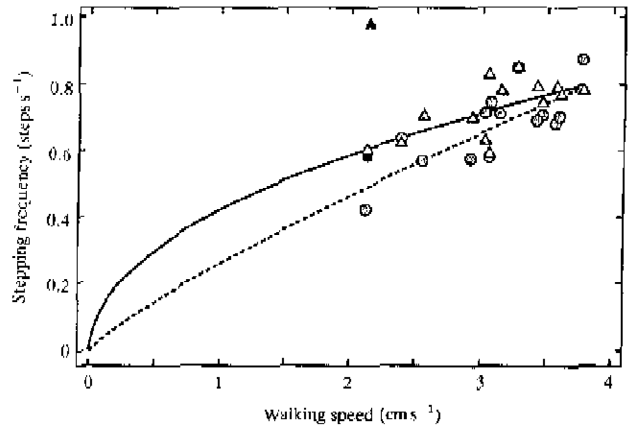

Fig. 5. The relationship of stepping frequency to walking speed for shore crabs travelling over rocky terrain in air. Triangles and solid line are for the leading leg row; circles and dashed line are for the trailing leg row; equations describing lines are given in Table 2; sample size is 15; each point represents an average value computed from 9–16 steps (mean=12.4 steps; s.d.=2.18 steps). Filled symbols were not used in computations for the lines.

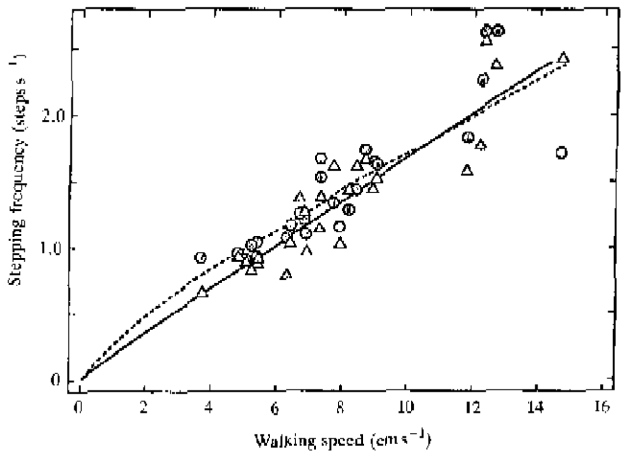

Fig. 6. The relationship of stepping frequency to walking speed for shore crabs travelling over smooth terrain while submerged. Triangles and solid line are for the leading leg row; circles and dashed line are for the trailing leg row; equations describing lines are given in Table 2; sample size is 25; each point represents an average value computed from 5–20 steps (mean=12.4 steps; s.d.=3.42 steps).

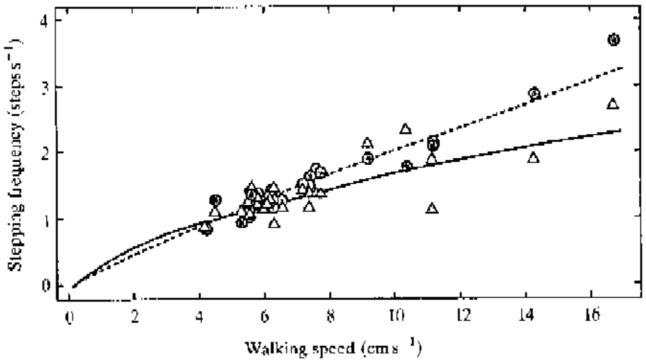

Fig 7. The relationship of stepping frequency to walking speed for shore crabs travelling over rocky terrain while submerged. Triangles and solid line are for the leading leg row; circles and dashed line are for the trailing leg row; equations describing lines are given in Table 2; sample size is 25; each point represents an average value computed from 7–19 steps (mean=12.7 steps; S.D.=2.75 steps).

Table 4. *Step lengths (mm) of* Pachygrapsus crassipes *when walking in different conditions*

Condition (regime, terrain, leg row)	Mean	±S.D.	Range	*N*
Air, smooth, leading	54.9	6.64	41.3–65.8	17
Air, smooth, trailing	51.7	4.63	43.5–59.2	17
Air, rocky, leading	41.8	5.86	29.5–51.8	15
Air, rocky, trailing	47.2	4.32	42.3–56.9	15
Submerged, smooth, leading	60.2	10.59	45.0–91.6	25
Submerged, smooth, trailing	53.9	9.10	44.0–85.7	25
Submerged, rocky, leading	51.5	8.24	33.1–68.8	25
Submerged, rocky, trailing	49.7	6.53	33.4–60.9	25

Only the anterior six walking legs are considered.
N, number of sequences.

Mann–Whitney test, $P<0.03$; Table 1). There was no significant relationship with walking speed (r^2 range 0.00–0.39 for all four conditions), possibly due partly to the large variability of the duty factor at the lower speeds and the small sample size at the higher speeds (Fig. 8).

The stances differed significantly among conditions (two-sided Mann–Whitney test, $P<0.005$). The widest and narrowest stances occurred in air while the two conditions of the submerged regime had stances closer together and between the values for the air regime (Table 3). Stance did not change with walking speed (r^2 range 0.01–0.22 for all conditions).

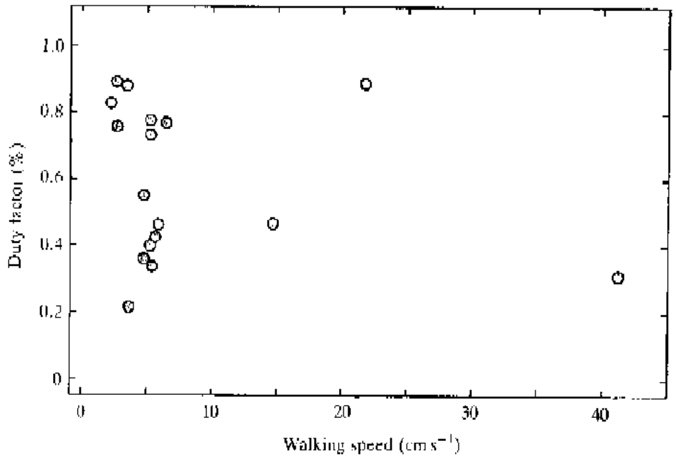

Fig. 8. Example of the variability of duty factor (fraction of the stepping cycle during which the dactyl is in contact with the substratum) values relative to walking speed of shore crabs. These data (N=17) are for the trailing leg row when on smooth terrain in air. The obvious variability is similar when walking under the other test conditions. There is no significant relationship between walking speed and duty factor in any condition.

Buoyancy eliminated over 80% of in-air weight when the crabs were submerged. One group lost 83.5% of its in-air weight while the other lost 85.0%. The difference may be due to incomplete filling of the branchial chamber when immersed for measurement. These results indicate a specific gravity of 1.2 for these shore crabs.

Discussion

Because I made no effort to examine the full range of walking speeds for these crabs under any of the conditions, these speed ranges are probably not representative of the crabs' abilities. Therefore, my interpretations of speed-related behaviours are conservative and may be shown to be erroneous by subsequent studies. However, because the overlap of the ranges is so extensive, comparison of the walking variables for each of the different conditions seems reasonable.

Pachygrapsus crassipes obviously modify walking variables according to regimes and terrain. Although various aspects of the crabs' ecology may be the causes of these modifications, the behaviours are consistent with a locomotion paradigm. The primary habitat of rocky shores (Hiatt, 1948; Gross, 1957) carries with it a risk of accidental damage to carapace or appendage due to a mis-step. Therefore, the walking modifications may be to maximize ease of walking and to minimize risk of injury.

The rocky terrain in air offered the highest risk and the crabs displayed the slowest walking speeds and the narrowest stances. The narrow stance may be to maximize the distance between the body and the uneven, unpredictable surface. Such a surface is more likely to injure the body in the event of a mis-step. The narrow stance also offers stability by allowing a step-length reserve: if a satisfactory foot-hold does not occur at an optimum short distance, the crab can lower its body to allow the dactylus to extend farther in its search for another site. By lowering its body, the centre of gravity can remain within the boundaries of its base of support. This type of stability may be safer for the crab because it is functional under both standing and walking conditions but does not have the potential for falling that 'dynamic stability' has (Hildebrand, 1980). Because it has many legs, more dactyli can be in contact with the substratum as the duty factor increases. With more than three dactyli on the substratum, the base of support expands from a triangle to a polygon of greater area. The larger area will reduce the opportunities for the crab's centre of gravity to move beyond its base of support. Therefore, with its multiple legs stepping in a metachronal pattern, the crab can increase its static stability by increasing its duty factor. The largest duty factor of all leg rows occurred over rocky terrain in air (Table 1), where poor stability may have the worst consequences in terms of accidental injury.

The effect of buoyancy when submerged reduces the risk of damage when over any terrain compared to being in air. This reduced risk is reflected in walking speeds, stances and duty factors. The speeds over rocky terrain were not reduced compared with those over smooth terrain. The stance over rocky terrain was wider than its counterpart in the air regime, perhaps because buoyancy reduces the strength required for standing, enabling obtuse angles in the leg joints to be maintained with less effort and simultaneously providing a lower profile that reduces interaction with drag forces of currents. Currents are reduced within the boundary layer that occurs at the substratum surface (Vogel, 1981). The duty factors were less than 46% for all leg rows over both submerged terrains. The larger duty factors of the trailing leg rows when submerged may be necessary to provide adequate thrust to counteract the drag forces encountered. Other crabs push with their trailing legs instead of pulling with their leading legs (Hafemann and Hubbard, 1969; Burrows and Hoyle, 1973).

When submerged, constant propulsive effort against drag forces may be more energetically efficient than intermittent effort for animals with rigid bodies (Weihs, 1974) and low fineness ratios (Blake, 1983) like these crabs. A phase difference of 50% for the trailing (propulsive) leg row would allow more uniform propulsive effort and is possible only over smooth terrain, because secure dactyli placement without searching is assured by the predictability of the terrain. This rationale is supported by results showing that the only condition in which the trailing row had a phase difference of 50% occurred over smooth terrain when submerged.

The forces needed to overcome locomotory drag can be roughly estimated and compared to the force needed to overcome gravity. Let us assume the following, Frontal area of the crab to the direction of motion (A) is $4\,\mathrm{cm}^2$; speed (U) is $10\,\mathrm{cm\,s^{-1}}$; drag coefficient (C_D) is 0.5 (blunt body with rounded corners); and the density of water (ρ) is $1000\,\mathrm{kg\,m^{-3}}$. Using drag $(D)=0.5\rho AC_DU^2$, $D=0.001\,\mathrm{N}$. If the crab has a mass of 35 g in air, then it has an underwater weight of 0.05 N ($0.035\,\mathrm{kg}$ in air $\times 9.8\,\mathrm{N\,kg^{-1}} \times 0.16$ negative buoyancy). Therefore, at the majority of underwater walking speeds I observed, the forces required to overcome drag appear to be approximately one order of magnitude lower than those required to overcome gravity.

Crabs apparently recognize the general nature of the terrain and remember the details as they encounter them, at least for the short term. The risk of injury due to a mis-step in air over rocky terrain would make learning more imperative there than over the other terrains. In air over rocky terrain the leading legs generally have shorter steps than the following legs (Table 3), a pattern to be expected if the crab is learning the irregularities with the leading legs but not the trailing legs. Consequently, the trailing legs can be placed directly on a known stable site and not used for tactile searching, resulting in a longer step length. Over smooth terrain in both regimes the leading legs do not need to search and, over rocky terrain in the submerged regime, buoyancy diminishes problems from mis-steps. Correspondingly, under these three conditions not requiring tactile searching, the leading legs take longer steps than do the trailing legs (Table 3). Neuromuscular activity of *Carcinus maenas* over smooth terrain in the two regimes also indicates longer steps by the leading legs (Clarac *et al.* 1987).

Vision plays an important role in ascertaining the general nature of the terrain (Hiatt, 1948). The eyes can be elevated and rotated in their stalks to maximize their visual capacity (Hiatt, 1948). However, because the eyes are located anteriorly and the crab walks sideways, the eyes may not be ideally located to view the terrain in the path of travel. Perhaps in partial compensation, the fourth leg of each side, located at the opposite end of the body from the eyes, is used for tactile feedback about the terrain and is not a consistent direct contributor to *P. crassipes* walking or to ghost crab running (Milne and Milne, 1946; Hafemann and Hubbard, 1969). The tactile feedback of the fourth legs can also be instrumental when the crab walks backwards and when it seeks refuge (Hiatt, 1948; Bovbjerg, 1960*a*).

Locomotion in two regimes is a key adaptation for shore crabs. The ability to walk from a submerged regime onto land requires adjustment to a sixfold increase in gravitational effects, an issue that must have been one of the first addressed to facilitate adaptations for terrestrial excursions. Terrestrial adaptations for dessication, respiration and thermal gradients can develop in small increments after the advent of terrestrial excursions. Real proficiency in terrestrial locomotion enables searching for separate bodies of water compatible with survival and propagation. Escape from the aquatic regime when dissolved oxygen decreases to levels approaching zero, as has been observed in coastal lagoons (Carpelin, 1961), offers survival. Escape to the terrestrial regime offers avoidance of aquatic predators and exposure of another habitat for foraging. Coastal lagoons may have afforded ideal conditions for the evolution of terrestrial crabs (Gross, 1961), but the ability to walk in both regimes must have been one of the first steps in that evolution.

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U.S. Department of the Interior

Certifications Regarding Debarment, Suspension and Other Responsibility Matters, Drug-Free Workplace Requirements and Lobbying

Persons signing this form should refer to the regulations referenced below for complete instructions:

Certification Regarding Debarment, Suspension, and Other Responsibility Matters - Primary Covered Transactions - The prospective primary participant further agrees by submitting this proposal that it will include the clause titled, "Certification Regarding Debarment, Suspension, Ineligibility and Voluntary Exclusion - Lower Tier Covered Transaction," provided by the department or agency entering into this covered transaction, without modification, in all lower tier covered transactions and in all solicitations for lower tier covered transactions. See below for language to be used; use this form for certification and sign, or use Department of the Interior Form 1954 (DI-1954). (See Appendix A of Subpart D of 43 CFR Part 12.)

Certification Regarding Debarment, Suspension, Ineligibility and Voluntary Exclusion - Lower Tier Covered Transactions - (See Appendix B of Subpart D of 43 CFR Part 12.)

Certification Regarding Drug-Free Workplace Requirements - Alternate I. (Grantees Other Than Individuals) and Alternate II. (Grantees Who are Individuals) - (See Appendix C of Subpart D of 43 CFR Part 12)

Signature on this form provides for compliance with certification requirements under 43 CFR Parts 12 and 18. The certifications shall be treated as a material representation of fact upon which reliance will be placed when the Department of the Interior determines to award the covered transaction, grant, cooperative agreement or loan.

PART A: Certification Regarding Debarment, Suspension, and Other Responsibility Matters - Primary Covered Transactions

CHECK__IF THIS CERTIFICATION IS FOR A PRIMARY COVERED TRANSACTION AND IS APPLICABLE.

(1) The prospective primary participant certifies to the best of its knowledge and belief, that it and its principals:

(a) Are not presently debarred, suspended, proposed for debarment, declared ineligible, or voluntarily excluded from covered transactions by any Federal department or agency;

(b) Have not within a three-year period preceding this proposal been convicted of or had a civil judgment rendered against them for commission of fraud or a criminal offense in connection with obtaining, attempting to obtain, or performing a public (Federal, State or local) transaction or contract under a public transaction; violation of Federal or State antitrust statutes or commission of embezzlement, theft, forgery, bribery, falsification or destruction of records, making false statements, or receiving stolen property;

(c) Are not presently indicted for or otherwise criminally or civilly charged by a governmental entity (Federal, State or local) with commission of any of the offenses enumerated in paragraph (1)(b) of this certification; and

(d) Have not within a three-year period preceding this application/proposal had one or more public transactions (Federal, State or local) terminated for cause or default.

(2) Where the prospective primary participant is unable to certify to any of the statements in this certification, such prospective participant shall attach an explanation to this proposal.

PART B: Certification Regarding Debarment, Suspension, Ineligibility and Voluntary Exclusion - Lower Tier Covered Transactions

CHECK__IF THIS CERTIFICATION IS FOR A LOWER TIER COVERED TRANSACTION AND IS APPLICABLE.

(1) The prospective lower tier participant certifies, by submission of this proposal, that neither it nor its principals is presently debarred, suspended, proposed for debarment, declared ineligible, or voluntarily excluded from participation in this transaction by any Federal department or agency.

(2) Where the prospective lower tier participant is unable to certify to any of the statements in this certification, such prospective participant shall attach an explanation to this proposal.

PART C: Certification Regarding Drug-Free Workplace Requirements

CHECK X IF THIS CERTIFICATION IS FOR AN APPLICANT WHO IS NOT AN INDIVIDUAL

Alternate I (Grantees Other Than Individuals)

A. The grantee certifies that it will or continue to provide a drug-free workplace by

(a) Publishing a statement notifying employees that the unlawful manufacture, distribution, dispensing, possession, or use of a controlled substance is prohibited in the grantee's workplace and specifying the actions that will be taken against employees for violation of such prohibition;

(b) Establishing an ongoing drug-free awareness program to inform employees about–
(1) The dangers of drug abuse in the workplace;
(2) The grantee's policy of maintaining a drug-free workplace;
(3) Any available drug counseling, rehabilitation, and employee assistance programs; and
(4) The penalties that may be imposed upon employees for drug abuse violations occurring in the workplace;

(c) Making it a requirement that each employee to be engaged in the performance of the grant be given a copy of the statement required by paragraph (a);

(d) Notifying the employee in the statement required by paragraph (a) that, as a condition of employment under the grant, the employee will --
(1) Abide by the terms of the statement; and
(2) Notify the employer in writing of his or her conviction for a violation of a criminal drug statute occurring in the workplace no later than five calendar days after such conviction;

(e) Notifying the agency in writing, within ten calendar days after receiving notice under subparagraph (d)(2) from an employee or otherwise receiving actual notice of such conviction. Employers of convicted employees must provide notice, including position title, to every grant officer on whose grant activity the convicted employee was working, unless the Federal agency has designated a central point for the receipt of such notices. Notice shall include the identification numbers(s) of each affected grant;

(f) Taking one of the following actions, within 30 calendar days of receiving notice under subparagraph (d)(2), with respect to any employee who is so convicted --
(1) Taking appropriate personnel action against such an employee, up to and including termination, consistent with the requirements of the Rehabilitation Act of 1973, as amended; or
(2) Requiring such employee to participate satisfactorily in a drug abuse assistance or rehabilitation program approved for such purposes by a Federal, State, or local health, law enforcement, or other appropriate agency;

(g) Making a good faith effort to continue to maintain a drug-free workplace through implementation of paragraphs (a) (b), (c), (d), (e) and (f).

B. The grantee may insert in the space provided below the site(s for the performance of work done in connection with the specific grant:

Place of Performance (Street address, city, county, state, zip code)
USGS/BRD Davis Field Station
One Shields Avenue, U.C. Davis
~~Kerr Hall, Room 278~~
Davis, CA 95616-5224

Check ___ if there are workplaces on file that are not identified here.

PART D. Certification Regarding Drug-Free Workplace Requirements

CHECK _ IF THIS CERTIFICATION IS FOR AN APPLICANT WHO IS AN INDIVIDUAL

Alternate II. (Grantees Who Are Individuals)

(a) The grantee certifies that, as a condition of the grant, he or she will not engage in the unlawful manufacture, distribution, dispensing, possession, or use of a controlled substance in conducting any activity with the grant;

(b) If convicted of a criminal drug offense resulting from a violation occurring during the conduct of any grant activity, he or she will report the conviction, in writing, within 10 calendar days of the conviction, to the grant officer or other designee, unless the Federal agency designates a central point for the receipt of such notices. When notice is made to such a central point, it shall include the identification number(s) of each affected grant.

PART E: Certification Regarding Lobbying
Certification for Contracts, Grants, Loans, and Cooperative Agreements

CHECK X IF CERTIFICATION IS FOR THE AWARD OF ANY OF THE FOLLOWING AND THE AMOUNT EXCEEDS $100,000: A FEDERAL GRANT OR COOPERATIVE AGREEMENT; SUBCONTRACT, OR SUBGRANT UNDER THE GRANT OR COOPERATIVE AGREEMENT.

CHECK __ IF CERTIFICATION IS FOR THE AWARD OF A FEDERAL LOAN EXCEEDING THE AMOUNT OF $150,000, OR A SUBGRANT OR SUBCONTRACT EXCEEDING $100,000, UNDER THE LOAN.

The undersigned certifies, to the best of his or her knowledge and belief, that:

(1) No Federal appropriated funds have been paid or will be paid, by or on behalf of the undersigned, to any person for influencing or attempting to influence an officer or employee of an agency, a Member of Congress, and officer or employee of Congress, or an employee of a Member of Congress in connection with the awarding of any Federal contract, the making of any Federal grant, the making of any Federal loan, the entering into of any cooperative agreement, and the extension, continuation, renewal, amendment, or modification of any Federal contract, grant, loan, or cooperative agreement.

(2) If any funds other than Federal appropriated funds have been paid or will be paid to any person for influencing or attempting to influence an officer or employee of any agency, a Member of Congress, an officer or employee of Congress, or an employee of a Member of Congress in connection with this Federal contract, grant, loan, or cooperative agreement, the undersigned shall complete and submit Standard Form-LLL, "Disclosure Form to Report Lobbying," in accordance with its instructions.

(3) The undersigned shall require that the language of this certification be included in the award documents for all subawards at all tiers (including subcontracts, subgrants, and contracts under grants, loans, and cooperative agreements) and that all subrecipients shall certify accordingly.

This certification is a material representation of fact upon which reliance was placed when this transaction was made or entered into. Submission of this certification is a prerequisite for making or entering into this transaction imposed by Section 1352, title 31, U.S. Code. Any person who fails to file the required certification shall be subject to a civil penalty of not less than $10,000 and not more than $100,000 for each such failure.

As the authorized certifying official, I hereby certify that the above specified certifications are true.

SIGNATURE OF AUTHORIZED CERTIFYING OFFICIAL Clifford A. Hui

TYPED NAME AND TITLE CLIFFORD A. HUI, Biologist/Principal Investigator

DATE 12 Apr 99

U. S. Department of the Interior
U. S. Geological Survey Biological Resources Division
Western Ecological Research Center
Davis Field Station
278 Kerr Hall
University of California
One Shields Ave.
Davis, California 95616-5224
(530) 752-6420 FAX (530) 752-8561

April 14, 1999

Mr. David Morrison, Resource Manager
Yolo County Planning Department
292 W. Beamer St.
Woodland, CA 95695

Dear Mr Morrison;

By this letter we are providing notification of that it is the intent of the Western Ecological Research Center of the Biological Resources Division, a division of the US Geological Survey, to submit a proposal to CALFED to conduct research studies within Yolo County. These studies will focus on the non-native invasive species known as the Chinese mitten crab. Although this crab is now distributed throughout most of the drainage system of the Sacramento River, these particular studies will be conducted in laboratories on the campus of the University of California in Davis. These studies focus on an aspect of walking biology of these crabs with the goal that the resultant information will facilitate the reduction and control of their populations.

If you have any questions, please contact me at the Davis field station: (530)752-6420.

Sincerely,

Clifford A. Hui

Clifford A. Hui, Ph.D.

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U. S. Geological Survey Biological Resources Division
Western Ecological Research Center
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USGS
science for a changing world

April 14, 1999

Members of the Yolo County Board of Supervisors
Board of Supervisors' Office
625 Court Street, Room 204
Woodland, CA 95695

Dear Board Members;

By this letter we are providing notification of that it is the intent of the Western Ecological Research Center of the Biological Resources Division, a division of the US Geological Survey, to submit a proposal to CALFED to conduct research studies within Yolo County. These studies will focus on the non-native invasive species known as the Chinese mitten crab. Although this crab is now distributed throughout most of the drainage system of the Sacramento River, these particular studies will be conducted in laboratories on the campus of the University of California in Davis. These studies focus on an aspect of walking biology of these crabs with the goal that the resultant information will facilitate the reduction and control of their populations.

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(530) 752-6420 FAX (530) 752-8561

April 14, 1999

Delta Protection Commission
14215 River Road
P.O. Box 530
Walnut Grove, California 95690

Dear Commission Members;

By this letter we are providing notification of that it is the intent of the Western Ecological Research Center of the Biological Resources Division, a division of the US Geological Survey, to submit a proposal to CALFED to conduct research studies with results which may affect the Delta. These studies will focus on the non-native invasive species known as the Chinese mitten crab, now distributed throughout most of the drainage system of the Sacramento and San Joaquin Rivers. These particular studies will be conducted in laboratories on the campus of the University of California in Davis. They will focus on an aspect of walking biology of these crabs with the goal that the resultant information will facilitate the reduction and control of crab populations.

If you have any questions, please contact me at the Davis field station: (530)752-6420.

Sincerely,

Clifford A. Hui, Ph.D.